

Published in final edited form as:

*Conscious Cogn.* 2015 March ; 32: 6–14. doi:10.1016/j.concog.2014.07.010.

## Speeded manual responses to unseen visual stimuli in hemianopic patients: What kind of Blindsight?

Alessia Celeghin<sup>1</sup>, Marissa Barabas<sup>1</sup>, Francesca Mancini<sup>1,2</sup>, Matteo Bendini<sup>3</sup>, Emilio Pedrotti<sup>1</sup>, Massimo Prior<sup>4</sup>, Silvia Savazzi<sup>1</sup>, and Carlo A. Marzi<sup>1</sup>

<sup>1</sup>Department of Neurological and Movement Sciences, University of Verona, Verona, Italy

<sup>2</sup>Rehabilitation Unit, Zevio Hospital, Verona, Italy

<sup>3</sup>Department of Neuroradiology, Treviso Hospital, Treviso, Italy

ASL 8 Asolo, Italy and University of Padua, Padua, Italy

### Abstract

Blindsight, i.e., unconscious visually guided behaviour triggered by stimuli presented to a cortically blind hemifield, has been typically found either by using direct (forced choice) or indirect (interhemispheric) methods. However, one would expect to find blindsight also in fast responses to suddenly appearing visual stimuli, a reminiscence of evolutionary ancient adaptive behaviour. In this study we provide preliminary evidence of this form of blindsight by using a conservative method for assessing blindsight based on a comparison between the cumulative probability functions (CPFs) of simple reaction times to blind and intact field stimuli. Furthermore, in two patients with blindsight we provided evidence that their above-chance unconscious responses were likely to be triggered by the intact hemisphere.

### Keywords

Reaction Time; Interhemispheric Transfer; Perceptual Awareness; Poffenberger Paradigm

### Introduction

Homonymous hemianopia defines the loss of vision in the hemifield contralateral to a lesion affecting the central visual pathways either at the level of optic tract (OT), optic radiation (OR) or primary visual cortex (V1). Hemianopia persisting after the unspecific symptoms of brain damage have vanished is usually long lasting or permanent (Zhang, Kedar, Lynn, Newmann, Biousse, 2006; Zihl, 2011) with heavy consequences for the patients' daily life. Importantly, following the pioneering studies of Poeppel, Held, and Frost (1973) and of Weiskrantz, Warrington, Sanders and Marshall (1974), it has been found that some degree of unconscious visually guided behaviour is possible when visual stimuli are presented to the blind hemifield. This phenomenon has been termed "blindsight" by Weiskrantz and co-

---

\*Corresponding author: Carlo A. Marzi, Department of Neurological & Movement Sciences, Section of Physiology and Psychology, University of Verona 8 Strada le Grazie, I-37134 Verona, Italy. Tel.: +39 045 8027143, Fax: +39 045 2027279, carloalberto.marzi@univr.it.

workers (Weiskrantz et al., 1974; Weiskrantz, 1997). Subsequently, two types of blindsight have been distinguished, namely, Type 1 which is the classic kind with absolutely no conscious awareness and Type 2 in which the patient has the feeling that something has occurred in the blind field but without any perceptual awareness. As reviewed by Danckert and Rossetti (2005), in addition to numerous unconscious visual abilities unrelated to a motor response, blindsight patients have been found to be able to perform various visually guided actions including manual pointing or saccading at unseen stimuli or grasping objects. Moreover, in a bilaterally cortically blind patient it has been possible to demonstrate an ability to avoid obstacles (de Gelder, Tamietto, van Boxtel, Goebel, Sahraie, van den Stock, Stienen, Weiskrantz, Pegna 2008). However, evidence that hemianopics might be able to react quickly to brief visual stimuli in a simple reaction time (RT) paradigm without stimulus awareness is lacking. This kind of unconscious visual function represents a phylogenetically old kind of behaviour with clear survival value and is likely to be subserved by subcortical visual centres such as the superior colliculus (Leh, Ptito, Schonwiesner, Chakravarty, Mullen, 2010; Tamietto, Cauda, Corazzini, Savazzi, Marzi, Goebel, Weiskrantz, de Gelder, 2010. Importantly, it does not rely on a forced-choice neither is the result of an influence exerted by stimuli presented to the intact hemifield, as assessed by direct or indirect testing methods, respectively. Therefore it does not suffer from the possibility that above-chance unconscious responding is a result of a discrepancy between criteria used for assessing awareness and for forced-choice discrimination (Azzopardi and Cowey (1997, 1998); Lloyd, Abrahamyan, Harris, 2013; Overgaard, 2011; Overgaard, Fehl, Mourisden, Bergholt, Cleeremans, 2008) which might in some cases explain blindsight-like phenomena. Thus, the behaviour tested in the present study represents a ‘new’ form of blindsight Type 1 on the basis of the assumption that the decision to react quickly to unseen stimuli must have been made automatically and unconsciously without a choice.

An interesting question, so far somewhat overlooked, concerns the *time course*, i.e., the speed of RT of blindsight responses. For example, is the CPF of RT to unseen stimuli different from that of normally perceived visual stimuli or it is simply overall lengthened? In the present study our strategy has been to compare the CPF of quick simple responses to visual stimuli presented to either the intact or the blind field. The crucial aspect of this procedure was to ask patients to respond as quickly as possible on every trial to the visual stimuli be they presented to the intact or to the blind hemifield. Patients were not asked to make a choice between responding or not and this partly avoids the problem of a criterion bias, see the Discussion section.

Another related question that will be dealt with in this paper concerns the problem of which hemisphere triggers the above mentioned fast unconscious responses to visual stimuli. Are they triggered by the lesioned or by the intact hemisphere through an interhemispheric transfer?

To try and answer these questions we tested hemianopic patients in the Poffenberger paradigm (Poffenberger, 1912) , i.e. a simple RT task with visual stimuli presented to one or the other hemifield and manual responses performed with the hand ipsilateral or contralateral to the stimulated hemifield. As is well known, this paradigm is used to measure interhemispheric transmission time with a simple behavioural paradigm (see Marzi, 1999).

As mentioned above, the strategy followed to ascertain the presence of non-chance responding to blind field stimuli was to compare the CPF of RT for blind and intact field stimuli. As crucial controls we also plotted the CPF of RT for stimuli presented when the patients were blindfolded. Moreover, we made sure that blindsight responses were triggered by the visual stimuli rather than by the warning acoustic stimulus by comparing the CPF for different intervals between the acoustic warning and the visual stimulus. For studying interhemispheric transmission time we measured the so called crossed-uncrossed difference (CUD) which is obtained by subtracting the mean RT in the uncrossed hemifield – hand conditions from that of the crossed conditions. This difference is considered a reliable index of interhemispheric transmission time because the crossed condition requires an interhemispheric transfer while this is not the case in the uncrossed condition.

## Methods

### Patients

We tested six patients with a chronic hemianopic field loss (as assessed by computerized clinical perimetry) caused by a unilateral lesion in the visual centres, see Table 1. All patients but one had a lesion in the right hemisphere. Two patients had a lesion of the OT. The others had lesions of different location and extent but always encompassing visual cortical areas. None of the patients showed neuropsychological or psychiatric symptoms.

### Stimuli and Procedure

The stimulus consisted of a dark grey circle ( $1^\circ$  diameter) presented with an exposure duration of 80 ms along the horizontal meridian at an eccentricity of  $6.5^\circ$  with respect to the fixation cross. The luminance of the stimulus was  $0.82 \text{ cd/m}^2$ . The background was light grey with a luminance of  $11.42 \text{ cd/m}^2$ . Following a brief warning acoustic tone and after a randomized interval (temporal window: 300-700 ms) the visual stimulus was presented to the left (LVF) or right visual field (RVF) in a randomized order. For stimulus presentations to the intact visual hemifield patients were required to press the space bar of a PC keyboard as quickly as possible with the index finger of either hand in alternating blocks of trials. Accepted RT ranged from 140 to 800 ms. For presentations to the blind hemifield they were asked to press the space bar as quickly as possible on every trial following the acoustic warning tone. We made sure to present the stimulus in perimetrically blind portions of the field and after each block of trials we asked the patient whether he/she had any visual awareness of the stimulus. If this was the case we changed the stimulus position. In fact, in the six patients described in the present study this never occurred. The accepted RT to blind field stimuli ranged from 140 to 1200 ms. For each visual hemifield presentation there were 80 trials with the left and 80 trials with the right hand. Catch trials in which no visual stimulus was presented after the acoustic warning stimulus were randomly intermingled in every block. There were 10 such trials for each hemifield-hand condition. All patients were tested at least in two separate sessions but some of them were tested in additional sessions. The RTs were averaged across sessions. Patients were tested either monocularly (AS, SL, MR, DS) with each eye or binocularly (AG, EA). In the former case the RTs of each eye were pooled together in the CPF.

## Results

### Evidence of blindsight

The percentage of correct responses, i.e., those RTs falling within the accepted RT range, is shown in Table 2 (intact field: left side; blind field: right side) for each patient. For all patients it was much higher for the intact than the blind hemifield (mean 96.84% vs 45.67%). The mean percentage of the various types of errors in the blind hemifield was as follows, Omissions: 29.54%; Anticipations: 15.84%; Retardations: 8.95%.

Mean RT for each patient for the two hemifields is also shown in Table 2. Again, for all patients performance was higher for the intact hemifield with faster RT than for the lesioned side (324.43 vs 393.03) .

**Cumulative Probability Functions (CPFs)**—To analyze the CPF of RT to stimuli presented to the two hemifields we plotted the percentage of RT that fell in each of 6 classes of frequency obtained from percentiles after having excluded the initial and the last class. Given 6 classes, chance is 16.6% in each class, see Figures 1 and 2 which show the CPF of single patients for three conditions of stimulus presentation: i) intact hemifield, ii) blind hemifield, iii) blindfolded.

To assess the presence of blindsight we relied on three sources of evidence. First, the presence and extent of overlap of the CPF of RTs in response to stimuli in the intact versus blind hemifield and, second, the lack of overlap between the latter and the CPF of RT with occluded vision. The third source of evidence was provided by a comparison between the CPF of RT to stimuli presented with a short interval between acoustic and visual stimuli (300-500 ms) with that for stimuli presented at a longer interval (500-700). If unconscious responses are triggered by the visual stimuli one would not expect to find a shift in the peak of RT as a function of the acoustic-visual interval. In contrast, if responses are triggered or prompted by the acoustic warning stimulus their CPF ought to show a shift to the left for the longer and to the right for the shorter interval.

The two patients whose CPF is reported in Fig. 1 (AS, AG) are those that yielded clear signs of above-chance responding in the blind hemifield for all three criteria mentioned above. It is evident that in AS (lower left graph) the CPF showed a partial but substantial overlap of intact and blind hemifields. This was not the case with eyes patched. Moreover, the lower right graph shows that the peak of RT following stimuli to the blind field did not shift with the two intervals.

Broadly similar evidence of blindsight for the three criteria is present in patient AG (upper row of graphs) in whom there is i) an overlap between responses to intact and blind field, particularly for the longer interstimulus interval, ii) a lack of overlap with occluded vision and ii) a lack of interval-related shift in the peak of blind field responses (upper right graph (Fig. 1.))

The above three criteria for the presence of blindsight were not fulfilled in the other four patients, see Fig. 2. In particular, the peak of responses in the blind hemifield shifted to the

left for the longer and to the right for the shorter interval. This means that the responses were related to the acoustic warning rather than to the visual stimulus.

One important question concerns the commonalities between the two patients displaying evidence of blindsight. As to behavioural performance the two patients' proportion of correct responses in the blind field was the highest (70.4%) for AG and the lowest for AS (27.2%) and therefore response accuracy does not seem to be related to the occurrence of blindsight.

Another obvious common factor might be the lesion: As shown in Fig. 3, AG has a large right temporo-occipital lesion including part of the calcarine cortex while AS (Fig. 4) has a unilateral right OT damage, i.e., two very different lesions. A similar consideration applies to RT. One common aspect is that as shown in Figs. 3 and 4 both patients with full field checkerboard stimulation show activation strictly limited to the visual cortex of the intact hemisphere and this is in keeping with the behavioural results described in the next section.

### **Which hemisphere subserves unconscious responses?**

A second question that we tackled in the two above patients exhibiting blindsight concerns which hemisphere subserves the motor response to the unconsciously detected stimuli.

To do that, we analyzed the CUD a behavioural measure that is considered as an estimate of callosal interhemispheric transfer time (for reviews see Marzi, 1999; Marzi, Bisiacchi, Nicoletti, 1991; Zaidel and Iacoboni, 2003). The classic procedure involves subtracting the mean RT of the two uncrossed hemifield-hand conditions from that of the two crossed-hemifield hand conditions. In healthy participants this subtraction consistently yields a positive CUD in the range of 3-5 ms, a value which is extremely lengthened in patients which lack the corpus callosum for genetic absence or surgical removal. This provides rather convincing evidence in favour of the original Poffenberger interpretation of the CUD, namely that the crossed (interhemispheric) condition requires a commissural extra step hence a longer RT with respect to the uncrossed (intrahemispheric) condition.

The rationale of our analysis in the hemianopic patients is straightforward: If blindsight is subserved by the lesioned hemisphere RT to blind field stimuli ought to be faster with the ipsilateral than with the contralateral hand because there is no need for an interhemispheric transfer i.e., one should obtain a positive CUD. In contrast, if blindsight is subserved by the intact hemisphere one should obtain a negative CUD for stimuli presented to the blind hemifield because paradoxically the uncrossed condition would necessitate a double interhemispheric transfer: One for transfer to the intact hemisphere of information on the occurrence of the stimuli and the other for accessing the ipsilesional motor centres for response, see Fig.5 for a schematic explanation.

This hypothesis relies on the assumption that in order to detect the occurrence of the stimuli they have to be transferred to the intact hemisphere at some level either visual or pre-motor. This, of course cannot easily be ascertained with purely behavioural tests. Some clues come from a recent magnetoencephalography (MEG) recording study (Ioannides, Poghossyan, Liu, Saridis, Tamietto, Op de Beeck, De Tège, Weiskrantz, de Gelder, 2012) showing the

complexity of the spatiotemporal processing of visual stimuli presented to the blind hemifield of blindsight patient GY involving multiple feed-back loops between higher level visual and non visual areas. This suggests that our hypothesized interhemispheric transfer from lesioned to intact hemisphere might occur at various commissural levels. At any rate, whatever level of transfer is involved, in the blind field condition there should be a negative CUD.

Fig.6 shows that in both patients there is evidence of a reliable CUD that is positive for the intact hemifield and negative for the blind hemifield and this represents evidence that the blindsight response was triggered by the intact hemisphere, as hypothesized. Interestingly, both the positive and the negative CUDs are larger than those typical of healthy participants showing that in the intact field interhemispheric transfer is abnormal (about 3 times longer than in healthy individuals) and in the blind field is about five times longer. These are important points concerning the dynamics of interhemispheric transmission that will be dealt with in a forthcoming study with event related potential (ERP) recording during performance of the Poffenberger paradigm.

Of course there are other possible interpretations of a negative CUD for the blind hemifield. One is that uncrossed hemifield-hand responses controlled by the lesioned hemisphere might use the ipsilateral cortico-spinal motor pathway which is notoriously smaller and less efficient than the contralateral pathway. This would yield an advantage of the crossed hemifield-hand condition because despite the necessity of an interhemispheric transfer, this condition would use the more efficient crossed cortico-spinal pathway. Another factor that might affect the above CUD results might be spatial attention. When in the Poffenberger paradigm hemianopic patients are fixating the centre of the screen they might pay more attention to the hand on the same side as the intact hemifield than to the other hand despite that the response key was positioned in a central position. This might yield an advantage of the hand contralateral to the field defect hence a negative CUD. Of course, this possibility should be specifically tested by varying the attentional demand of the task. Finally, a negative CUD might be related to brain damage affecting the motor centres controlling the ipsilesional hand and causing an overall slowing down of RT with that hand. This possibility, however, was ruled out in our patients who showed no manual differences for RT to stimuli presented in central vision.

**General Discussion—**We used a new, conservative, method for testing blindsight, namely to compare the CPF of RT for stimulus presentation to the intact and the blind field under normal or occluded viewing conditions. The rationale is straightforward: if the two distributions overlap within values of RT that exclude anticipations or retardations, then we are entitled to postulate the existence of unconscious above chance responses in the blind field. Of course, one might argue that this overlap might be related to the patient guessing the acceptable range of visual stimulus onsets but in such improbable event it is difficult to explain the difference between crossed and uncrossed conditions. Furthermore, the possibility that RT within the accepted range was triggered by the acoustic warning stimulus is ruled out by its relation with the latency of the visual stimulus.



It remains to be ascertained what are the factors enabling only two out of six patients to display this unconscious behaviour. The two patients with blindsight have different lesions: AS has a unilateral OT lesion, as a result of closed-head injury, see Fig. 4, hence a deafferentation of the whole cortical and subcortical ipsilesional visual centres. This is corroborated by fMRI evidence obtained with full field visual activation showing a strictly unilateral activation of the visual cortex (Fig. 4). Therefore, blindsight must be subserved by areas of the intact hemisphere containing a representation of parts of the ipsilateral hemifield. A likely candidate might be the SC although human fMRI studies have not found an ipsilateral representation (DuBois and Cohen, 2000; Katyal, Zughini, Greene, Ress, 2010; Schneider and Kastner, 2005). In contrast, a clear ipsilateral representation of the visual field is present in the SC of the cat as shown by Antonini, Berlucchi, Marzi and Sprague (1979) with single cell recording, a method, that apart from possible species differences, is more sensitive than fMRI for visual field mapping

Patient AG suffered from a different lesion, namely, a stroke in the territory of the posterior cerebral artery resulting in damage to mesial and basal temporal cortex, occipital cortex including the primary visual area as well as postero-inferior thalamus. In keeping with that, as with the other blindsight patient, fMRI with full field visual stimulation showed activation limited to the intact hemisphere. May be that for both patients an ipsilesional subcortical mediation of blindsight was made impossible. Even though the location of the lesion was different in both cases input to the SC was impeded .

An important question, which is relevant for the specific topic of this Special Issue, is whether the above-chance responses of two patients to stimuli presented to the blind hemifield can be considered as evidence of blindsight Type 2 rather than Type 1. The former term was coined by Weiskrantz (1997) for patients who claim to have experienced during stimulus presentation a feeling of a change occurred within their blind area, e.g. movement, (see also Sahraie, Treveltham, Macleod, Weiskrantz, Hunt, 2013). Our patients were required to press a key as quickly as possible on every trial following blind field presentation in a simple RT paradigm, i.e. without a choice and presumably in a sort of automatic way. Thus, this behaviour is different from classic blindsight obtained in a forced-choice paradigm in which there is a “conscious choice” between unseen stimuli and time of response is irrelevant. Importantly, the above-chance unconscious responding found in the present study cannot be a measurement artefact of the use of a high response criterion under yes-no measures of visual awareness when compared with criterion free forced-choice responses as pointed out recently by Lloyd et al. (2013) in a study using TMS induced blindsight in healthy participants as well as previously by Azzopardi and Cowey (1997, 1998) and Overgaard (2011). We think that the patients’ response in our test was either prompted by the warning tone (and therefore was not evidence of blindsight) or was unconsciously triggered by the visual stimuli. The two possibilities could be dissociated by our analysis of the CPF as a function of the interval between acoustic warning and visual stimulus. In the latter case it might be considered as a form of blindsight different from both Type 1 and Type 2. Broadly similar evidence has been recently gathered by recording the dwell time of saccades, i.e. the mean percentages of gaze positions directed to stimulus areas rendered invisible by continuous flash suppression (Rothkirch, Stein, Sekutowicz, Sterzer, 2012). Dwell times for the stimulus area were on average increased by 40% relative to the control

area despite detection performance was at chance. This is clearly a demonstration of automatically triggered oculo-motor behaviour in absence of perceptual awareness in healthy individuals that can be broadly assimilated to the (manual) motor response automatically triggered by stimuli presented to the blind hemifield in our blindsight patients. Further evidence for an automatic triggering of motor responses by visual stimuli comes from the obstacle avoiding behaviour described in a cortically blind patient by deGelder et al. (2008) as well as from studies with subliminal stimuli in healthy participants (for a review see McBride, Boy, Husain, Sumner, 2012).

Summing up, we believe that the thrust of the present study is twofold: Firstly, it provides evidence of a 'new' form of blindsight tested with a simple RT paradigm requiring no choice and therefore less amenable to artefacts related to a dissociation between criteria for scoring levels of awareness and forced choice discriminations. Secondly, it provides preliminary behavioural evidence for a role of the intact hemisphere in subserving motor responses to unconscious visual stimuli.

## Acknowledgements

The study was supported by ERC grant 339939 "Perceptual Awareness" awarded to C.A. Marzi.

## References

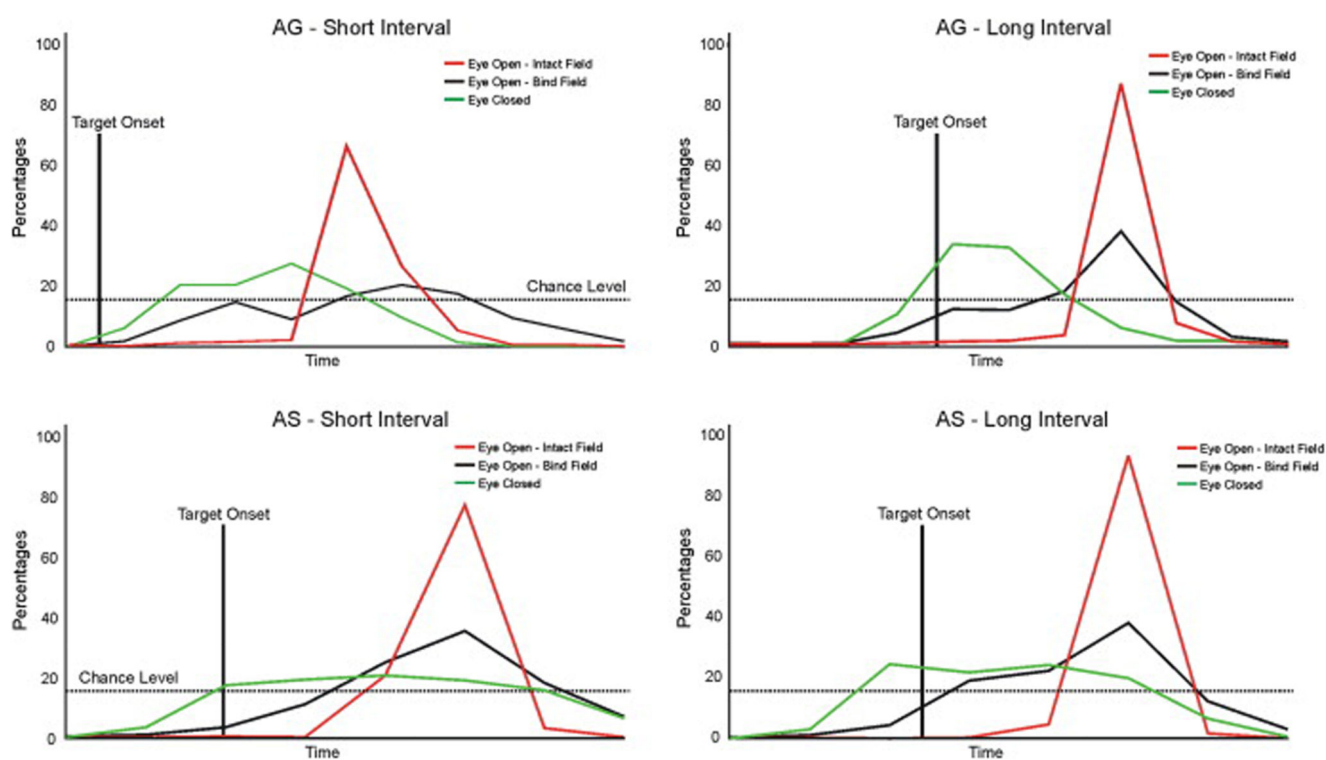
- Antonini A, Berlucchi G, Marzi CA, Sprague JM. Behavioral and electrophysiological effects of unilateral optic tract section in ordinary and Siamese cats. *The Journal of comparative Neurology*. 1979; 185(1):183–202. [PubMed: 429613]
- Azzopardi P, Cowey A. Is blindsight like normal near-threshold vision? *Proceedings of the National Academy of Sciences of the United States of America*. 1997; 94(25):14190–14194. [PubMed: 9391175]
- Azzopardi P, Cowey A. Blindsight and Visual Awareness. *Consciousness and cognition*. 1998; 7(3): 292–311. [PubMed: 9787046]
- Berlucchi G, Aglioti S, Marzi CA, Tassinari G. Corpus callosum and simple visuomotor integration. *Neuropsychologia*. 1995; 33(8):923–936. [PubMed: 8524454]
- Berlucchi G. Visual interhemispheric communication and callosal connections of the occipital lobes. *Cortex*. 2013; doi:pii: S0010-9452(13)00037-3 [Epub ahead of print]. doi: 10.1016/j.cortex. 2013.02.001
- Danckert J, Rossetti Y. Blindsight in action: what can the different sub-types of blindsight tell us about the control of visually guided actions? *Neuroscience and Biobehavioral Review*. 2005; 29(7):1035–1046.
- de Gelder B, Tamietto M, van Boxtel G, Goebel R, Sahraie A, van den Stock J, Stienen BM, Weiskrantz L, Pegna A. Intact navigation skills after bilateral loss of striate cortex. *Current Biology*. 2008; 18(24):R1128–1129. [PubMed: 19108766]
- Dodds C, Machado L, Rafal R, Ro T. A temporal/nasal asymmetry for blindsight in a localisation task: evidence for extrageniculate mediation. *Neuroreport*. 2002; 13(5):655–658. [PubMed: 11973465]
- DuBois RM, Cohen MS. Spatiotopic organization in human superior colliculus observed with fMRI. *Neuroimage*. 2000; 12(1):63–70. [PubMed: 10875903]
- Iacoboni M, Zaidel E. Channels of the corpus callosum. Evidence from simple reaction times to lateralized flashes in the normal and the split brain. *Brain*. 1995; 118(Pt 3):779–788. [PubMed: 7600094]
- Ioannides AA, Poghosyan V, Liu L, Saridis GA, Tamietto M, Op de Beeck M, De Tière X, Weiskrantz L, de Gelder B. Spatiotemporal profiles of visual processing with and without primary visual cortex. *Neuroimage*. 2012; 63(3):1464–1477. [PubMed: 22877580]



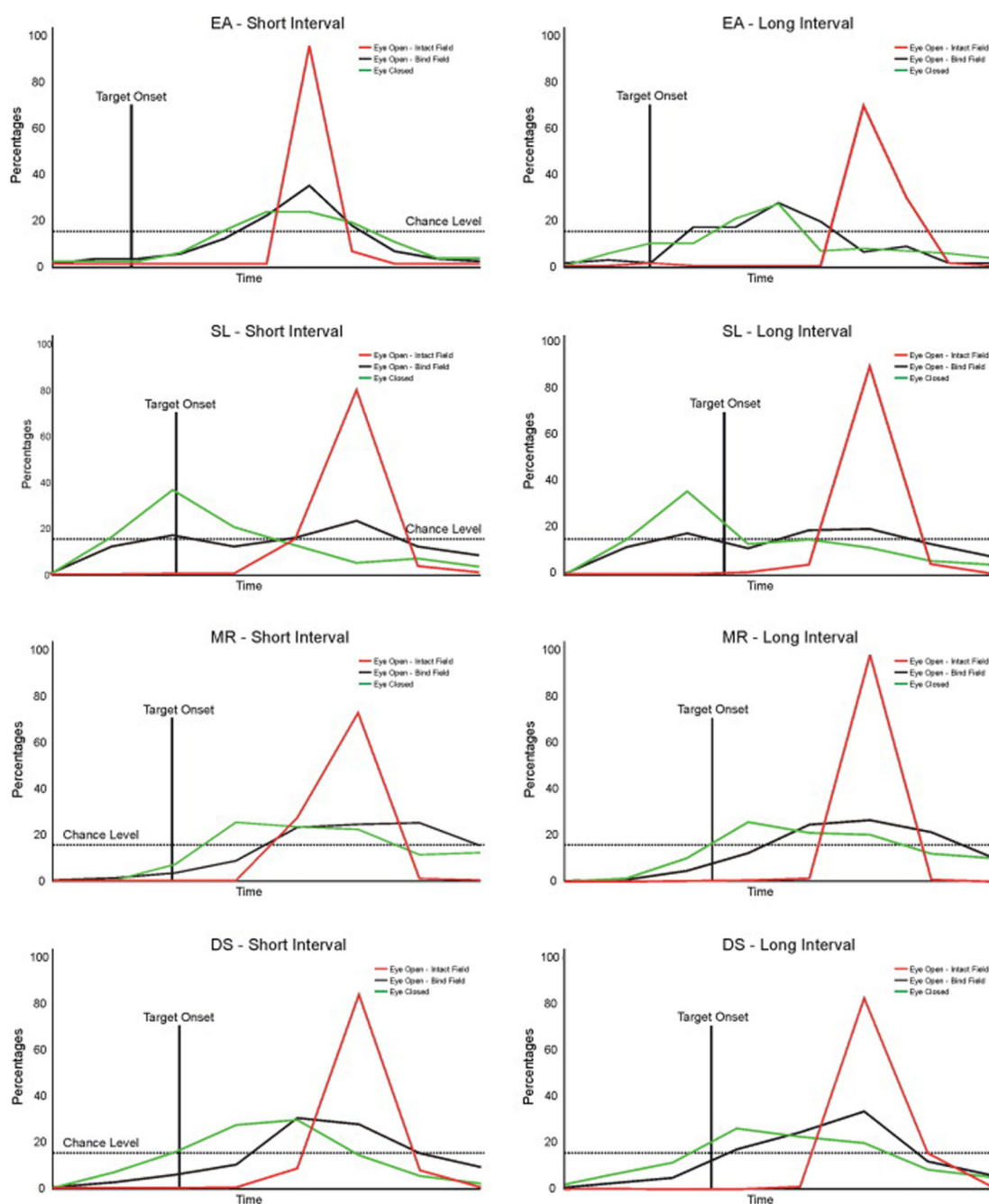
- Katyal S, Zughni S, Greene C, Ress D. Topography of covert visual attention in human superior colliculus. *Journal of Neurophysiology*. 2010; 104(6):3074–3083. [PubMed: 20861435]
- Leh SE, Ptito A, Schönwiesner M, Chakravarty MM, Mullen KT. Blindsight mediated by an S-Cone-independent collicular pathway: an fMRI study in hemispherectomized subjects. *Journal of Cognitive Neuroscience*. 2010; 22(4):670–682. [PubMed: 19309296]
- Lloyd DA, Abrahamyan A, Harris JA. Brain-stimulation induced blindsight: unconscious vision or response bias? *PLoS One*. 2013; 8(12):e82828.doi: 10.1371/journal.pone.0082828 [PubMed: 24324837]
- Marzi CA. The Poffenberger paradigm: a first, simple, behavioural tool to study interhemispheric transmission in humans. *Brain Research Bulletin*. 1999; 50(5-6):421–422. [PubMed: 10643464]
- Marzi CA, Bisiacchi P, Nicoletti R. Is interhemispheric transfer of visuomotor information asymmetric? Evidence from a meta-analysis. *Neuropsychologia*. 1991; 29(12):1163–1177. [PubMed: 1838793]
- McBride J, Boy F, Husain M, Sumner P. Automatic motor activation in the executive control of action. *Frontiers in Human Neuroscience*. 2012; 6(82):1–14. [PubMed: 22279433]
- Milner AD, Lines CR. Interhemispheric pathways in simple reaction time to lateralized light flash. *Neuropsychologia*. 1982; 20(2):171–179. [PubMed: 6283415]
- Moscovitch M, Smith LC. Differences in neural organization between individuals with inverted and noninverted handwriting postures. *Science*. 1979; 205(4407):710–713. [PubMed: 462180]
- Overgaard M, Fehl K, Mouridsen K, Bergholt B, Cleeremans A. Seeing without seeing? Degraded conscious vision in a blindsight patient. *PLoS One*. 2008; 3(8):e3028.doi: 10.1371/journal.pone.0003028 [PubMed: 18716654]
- Overgaard M. Visual experience and blindsight: a methodological review. *Experimental Brain Research*. 2011; 209(4):473–479. [PubMed: 21327769]
- Poffenberger AT. Reaction time to retinal stimulation with special reference to the time lost in conduction through nervous centers. *Archives of Psychology*. 1912; 23:1–73.
- Poeppl E, Held R, Frost D. Residual visual function after brain wounds involving the central visual pathways in man. *Nature*. 1973; 243(5405):295–296. [PubMed: 4774871]
- Rothkirch M, Stein T, Sekutowicz M, Sterzer P. A direct oculomotor correlate of unconscious visual processing. *Current Biology*. 2012; 22(13):R514–515. [PubMed: 22789995]
- Sahraie A, Trevethan CT, Macleod MJ, Weiskrantz L, Hunt AR. The continuum of detection and awareness of visual stimuli within the blindfield: from blindsight to the sighted-sight. *Investigative Ophthalmology & Visual Science*. 2013; 54(5):3579–3585. [PubMed: 23633654]
- Schneider KA, Kastner S. Visual responses of the human superior colliculus: a high-resolution functional magnetic resonance imaging study. *Journal of Neurophysiology*. 2005; 94(4):2491–2503. [PubMed: 15944234]
- Smith LC, Moscovitch M. Writing posture, hemispheric control of movement and cerebral dominance in individuals with inverted and noninverted hand postures during writing. *Neuropsychologia*. 1979; 17(6):637–644. [PubMed: 522977]
- Tamietto M, Cauda F, Corazzini LL, Savazzi S, Marzi CA, Goebel R, Weiskrantz L, de Gelder B. Collicular vision guides nonconscious behavior. *Journal of Cognitive Neuroscience*. 2010; 22(5):888–902. [PubMed: 19320547]
- Weiskrantz L. *Consciousness Lost and Found: A Neuropsychological Exploration*. Oxford: University Press; 1997.
- Weiskrantz L, Warrington EK, Sanders MD, Marshall J. Visual capacity in the hemianopic field following a restricted occipital ablation. *Brain*. 1974; 97(4):709–728. [PubMed: 4434190]
- Zaidel, E.; Iacoboni, M. Introduction: Poffenberger's simple reaction time paradigm for measuring interhemispheric transfer time. The parallel brain. The cognitive neuroscience of the corpus callosum. Zaidel, E.; Iacoboni, M., editors. Cambridge, Mass: MIT Press; 2003. p. 1-7.
- Zhang X, Kedar S, Lynn MJ, Newman NJ, Biousse V. Natural history of homonymous hemianopia. *Neurology*. 2006; 66(6):901–905. [PubMed: 16567709]
- Zihl, J. *Rehabilitation of Visual Disorders After Brain Injury*. 2nd edition. Hove, East Sussex: Psychology Press;

### Highlights

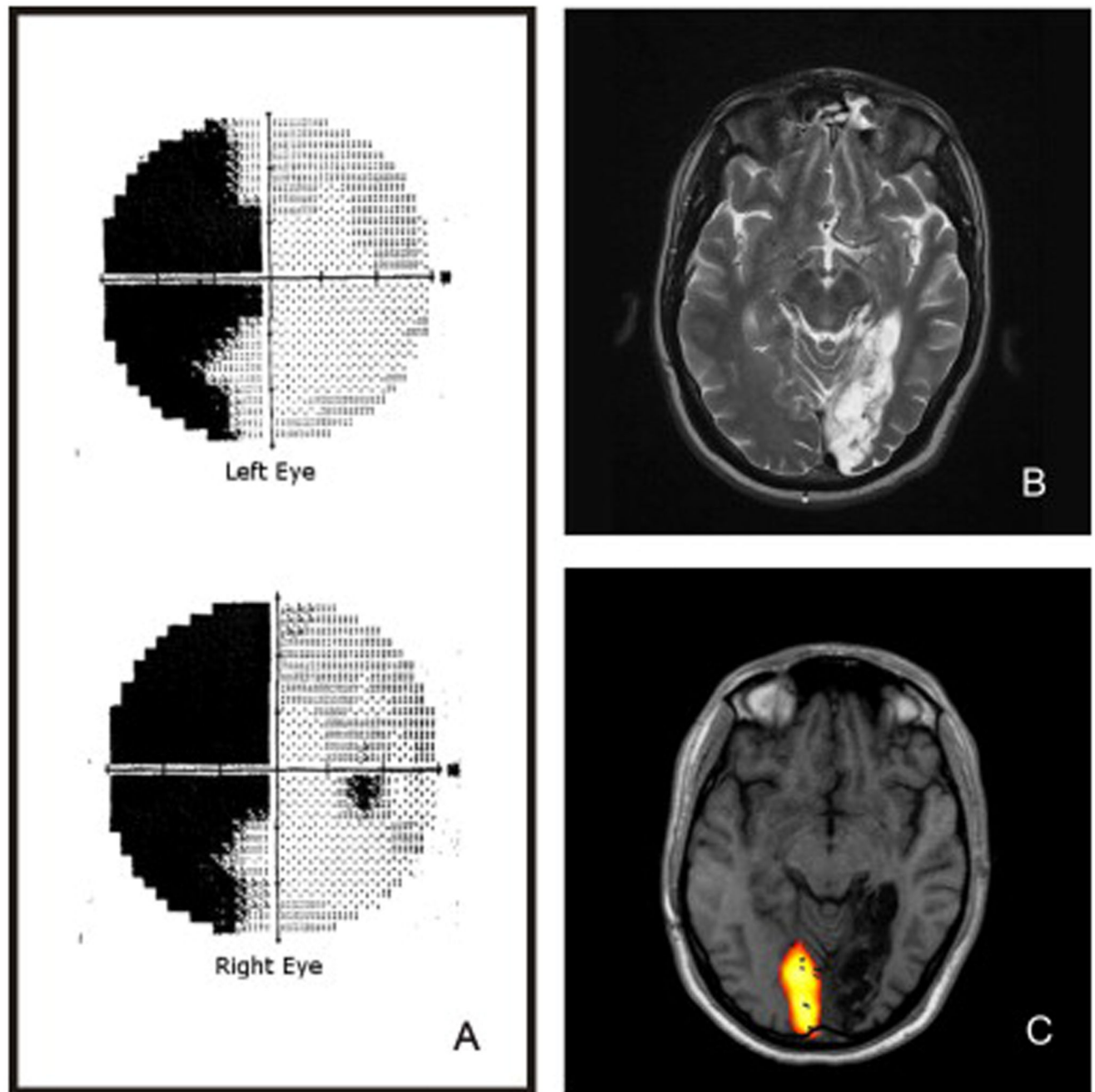
- We tested a new form of blindsight consisting of speeded manual response to unperceived visual stimuli
- This test is free form choice decisional biases
- We provided behavioural evidence that this kind of blindsight is subserved by the intact hemisphere



**Figure 1.** CPF for patients AG (upper row) and AS (lower row) for short (left graphs) and long (right graphs) intervals between acoustic warning and visual stimulus. See text for description of the results

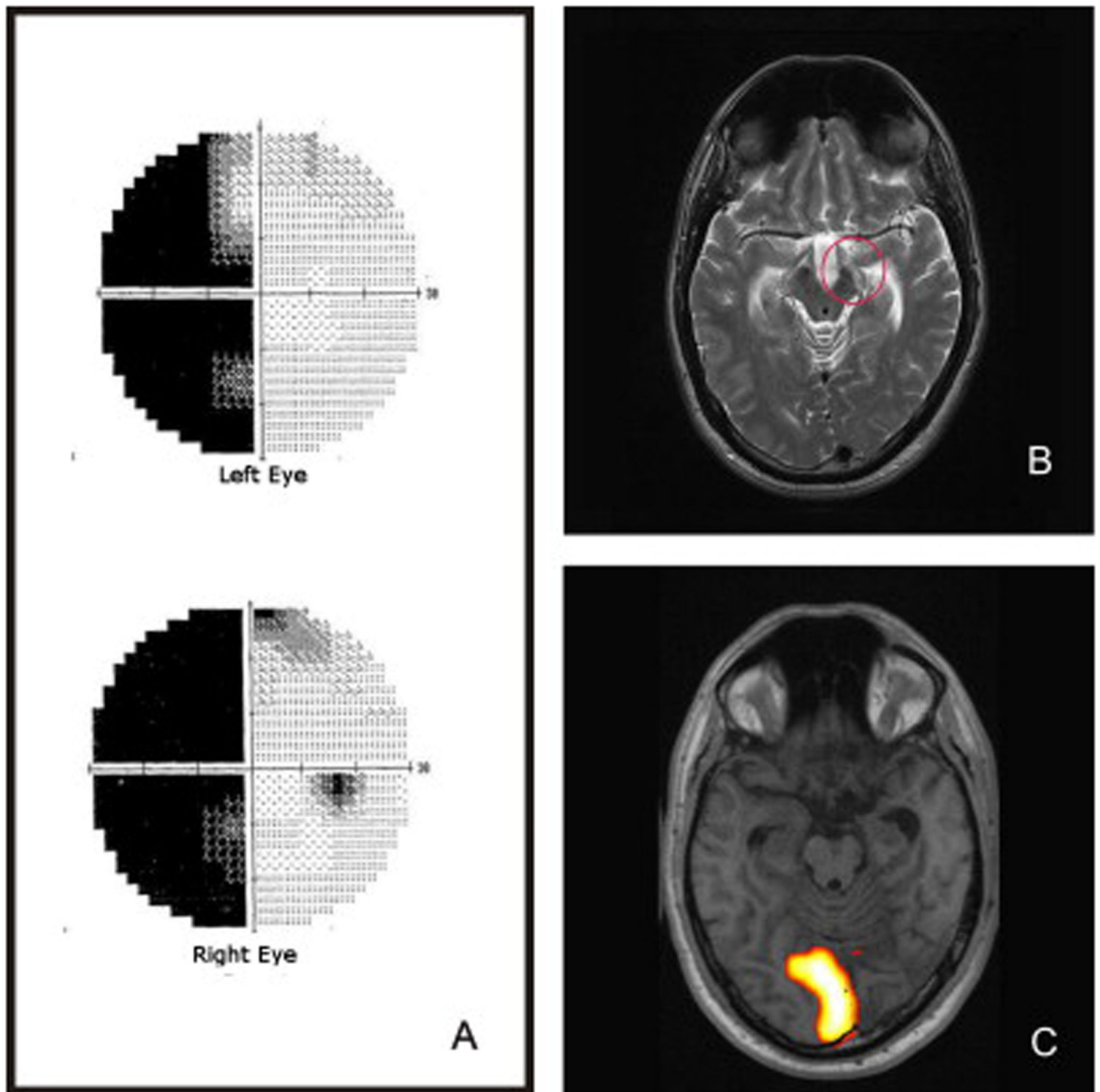


**Figure 2.**  
CPF for patients not showing blindsight. See text for description of the results



**Figure 3.**

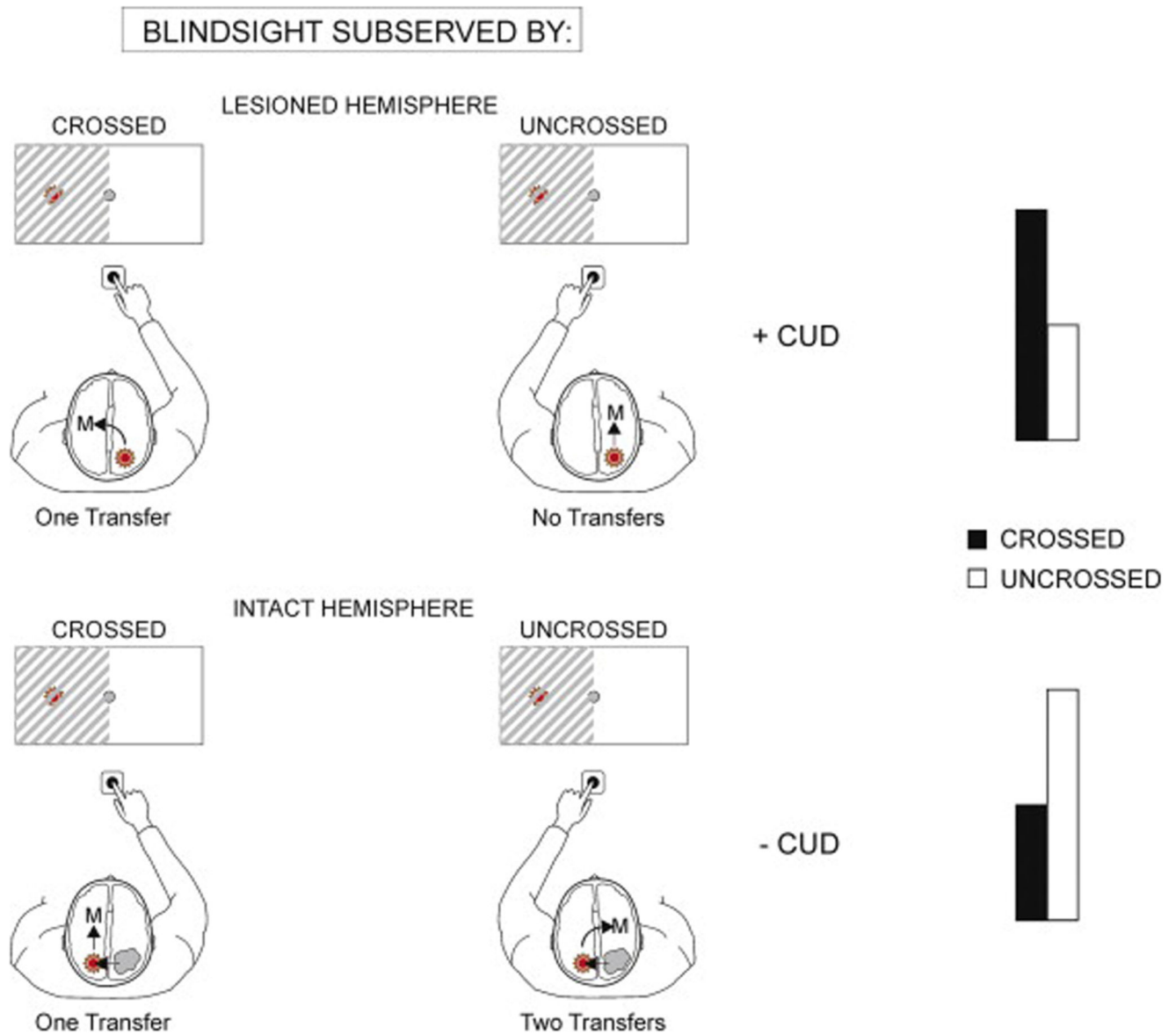
Patient AG. A: Monocular visual fields showing a typical hemianopic loss with some sparing of a medial area in the lower quadrant and a smaller medial area in the upper quadrant of the left eye while in the right eye there is a spared area only in the medial part of the lower quadrant. Note that the visual stimuli were presented well outside those areas. B: MRI section showing a large right hemisphere lesion in the temporal and occipital lobe including the calcarine fissure. C: fMRI, full field visual field stimulation with checkerboards showing activation of only the contralesional visual cortex



**Figure 4.**

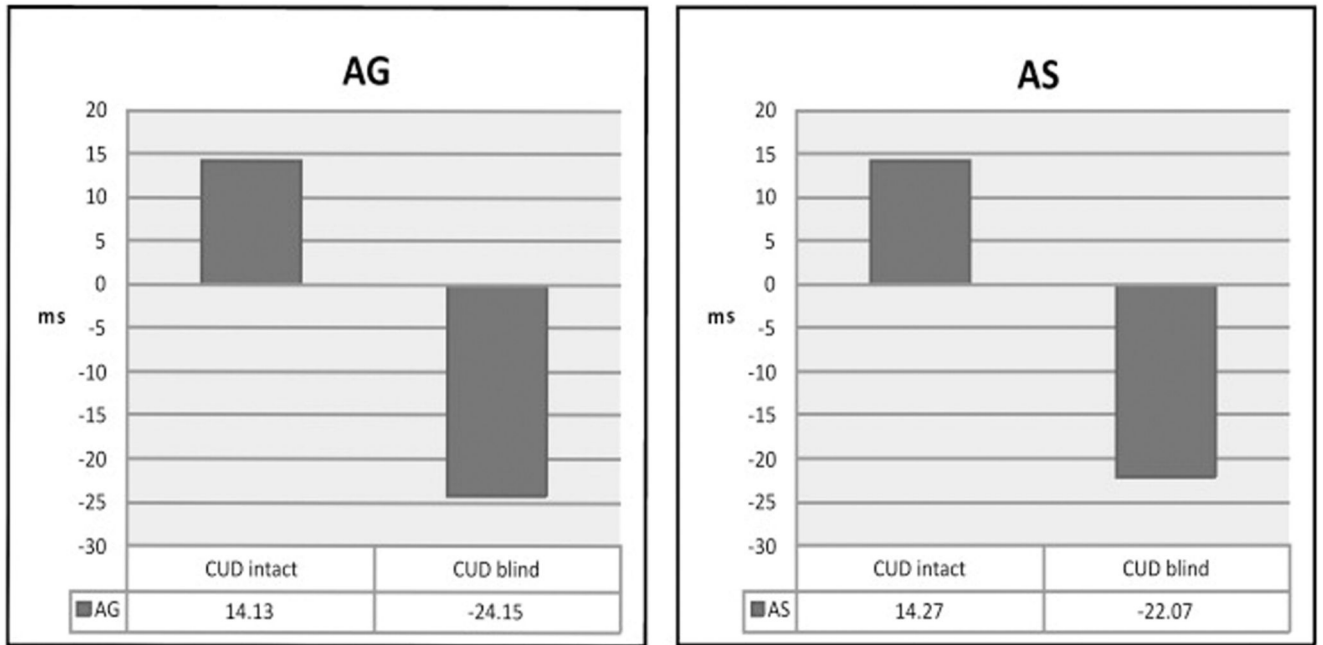
Patient AS. A: Monocular visual fields showing a typical hemianopic loss with some sparing in the upper and lower quadrant of the left eye and in the lower quadrant of the right eye. Note that the visual stimuli were presented well outside those areas. B: MRI section showing an abnormal OT on the left side (indicated by a red ring). C: fMRI, full field visual field stimulation with checkerboards showing activation of only the contralesional visual cortex





**Figure 5.**

Schema illustrating the different number of interhemispheric transfers occurring for stimulus presentations to the blind hemifield when blindsight is subserved by the lesioned (upper drawings) or by the intact hemisphere (lower drawings), see text for explanation.



**Figure 6.**

Histograms showing the CUDs for the two patients with blindsight when stimuli are presented to the intact or blind field. Note that in both patients the CUDs are negative for the blind field and positive for the intact field.

**Table 1**

	<b>GENDER</b>	<b>AGE</b>	<b>HEMIANOPIA</b>	<b>ETIOLOGY</b>	<b>LESION</b>
SL	F	44	Right	Ischemic stroke with hemorrhagic evolution	left mesial-occipital lobe including calcarine area
AS	M	30	Left	Closed head trauma	Right optic tract
MR	M	23	Left	Closed head trauma	Right optic tract
SD	M	34	Left	Arteriovenous malformation	Right optic radiation
AG	M	36	Left	Ischemic Stroke	Right temporo-occipital lobe including part of calcarine area
EA	M	60	Left	Ischemic Stroke	Right mesial-occipital lobe including part of optic radiation

**Table 2**

	Percent Correct Response		Reaction Times	
	Intact Hemifield	Blind Hemifield	Intact Hemifield	Blind Hemifield
SL	93.53	32.95	320.89	436.79
AS	94.11	27.26	312.63	348.25
MR	99.05	54.67	329.53	432.79
DS	98.22	44.36	358.76	416.91
AG	96.46	70.41	331.07	403.10
EA	99.68	44.37	293.71	320.32
Mean	96.84	45.67	324.43	393.03



**Table 3**

Percent type of errors			
	%Omissions	%Anticipations	%Retardations
Intact Hemifield	1.20	0.85	1.11
Blind Hemifield	29.54	15.84	8.95

